

Lower Oligocene Amphibians from Saskatchewan

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MAINLY through the invention and maintenance of an ingenious matrix processing machine by personnel of the Saskatchewan Museum of Natural History, the list of more than 40 species of vertebrates known from the Cypress Hills formation of Saskatchewan is now beginning to burgeon with microvertebrates. Among the new remains are those of a salamander, *Ambystoma*, and three anurans, *Rhinophrynus*, *Scaphiopus*, and *Hyla*, whose fossil records are herein pushed back millions of years into the early Oligocene.

The locality lies along the north branch of Calf Creek, 10 miles northwest of Eastend, Saskatchewan, in Legal Subdivision 4, section 8, township 8, range 22 W. 3rd meridian. The elevation is 3,600 feet. Bones were first found in this formation in 1883 (McConnell, 1885), and collections have been made since then by many groups and individuals. Sites have been worked by the Royal Ontario Museum, the National Museum of Canada, and the Saskatchewan Museum of Natural History. Unfortunately, of late, some private individuals without affiliation with institutions that maintain collections have collected from the locality.

Bones reported on in the present paper are the result of systematic collecting of microvertebrates that has periodically been done since 1960 by field parties of the Saskatchewan Museum of Natural History. Bruce McCorquodale, A. E. Swanston, and R. D. Weigel were particularly instrumental in securing the fossils. Matrix was processed over several field seasons by a special machine maintained by the Museum, but in September of 1967, R. D. Weigel and J. A. Holman spent several days at the site collecting microvertebrates with hand-operated screens. The fossils were collected from a matrix of conglomeratic sandstones and sands, the richest matrix being that that included small clay pellets.

Russell (1948) indicates that the Cypress Hills formation is of early Oligocene age, and on the basis of its mammalian remains, indicates that it is equivalent to the lowest part of the Chadron formation of South Dakota. The sediments of the Cypress Hills formation originated in the Rocky Mountains to the southwest and were carried to their present location by streams. The presence of

deltas, created by streams emptying into temporary lakes, has been suggested.

Most of the larger fossils from the deposit represent bronto-theres, rhinoceri, a small three-toed horse, entelodonts, camels, antelopes, oreodonts, anthracotheres, small dogs, medium-sized saber-toothed cats, a bear-like carnivore, crocodiles, and turtles. The smaller vertebrate fossils consist mainly of fragmental remains of rodents, rabbits, insectivores, a small quail, a sandpiper, a cuckoo, lizards, boid snakes, catfishes, bowfins, and gars. Only one amphibian, the small burrowing anuran *Rhinophrynus canadensis*, has previously been reported from the deposit.

Early studies of the Cypress Hills include those of Cope (1891) and Lambe (1908); more recent studies include those of Russell (1934, 1936, 1938, 1940, and 1948); and the most recent papers are those of Holman (1963) and Weigel (1963) who respectively reported on the first amphibian and bird remains from the deposit. Dr. Loris Russell is presently planning additional studies on the new mammalian material, and I plan a forthcoming paper on the new reptilian remains.

I would here like to extend my appreciation to those members of the Saskatchewan Museum of Natural History who have so generously allowed me to study material collected and curated by them, especially Fred Bard, Bruce McCorquodale, and A. E. Swanson. Dr. Robert D. Weigel of Illinois State University helped collect and transport the bones and has provided invaluable information about the deposit. Dr. J. A. Tihen of Notre Dame University kindly discussed the generic identification of the salamander remains with me, and Dr. Richard Estes of Boston University identified the pelobatids as well as providing interesting comments about other aspects of the study. Dr. Charles Walker of the University of Michigan loaned recent skeletal material used in the study. My work was supported by National Science Foundation Grant GB-5988. Donna Rae Holman made the drawings.

Family AMBYSTOMATIDAE

This family is presently restricted to the New World, ranging from southern Alaska and Hudson Bay through the United States and south into Mexico on the Mexican Plateau.

The first record of the family is a paleocene trackway in Sweet-

grass County, Montana, described by Peabody (1954) as *Ambystomichnus montanus*. This salamander is thought to be similar to the living *Dicamptodon*, but it is twice as large. *Dicamptodon* is reported from the lower Pliocene on the basis of trackways (Peabody, 1959).

The genus *Ambystoma* is first recorded from beds that are transitional between uppermost Miocene and lowermost Pliocene times in Brown County, Nebraska by Tihen and Chantell (1963). This form, *Ambystoma minshalli* is said to be a member of the *maculatum* species group of Tihen (1958).

The middle Pliocene forms *Plioambystoma*, *Lanebatrachus*, and *Ogallalabatrachus* are thought to be synonyms of the middle Pliocene salamander *Ambystoma kansense* (Adams and Martin), a member of the *mexicanum* species group of Tihen (1958).

Only the living species *Ambystoma maculatum*, *A. texanum*, and *A. tigrinum* are known from Pleistocene deposits (Gehlbach, 1965, Holman, 1965).

Although the vertebrae of Ambystomatidae are relatively simple in structure, they have been rather widely used in fossil studies. The vertebrae of the Ambystomatidae have an amphicoelous centrum (opisthocelous in the Salamandridae and in some Plethodontidae) that lacks a ventral keel (ventrally keeled in Amphiumidae and Sirenidae). The transverse processes are weakly divided distally, but fused proximally (undivided in the Cryptobranchidae, some Hynobiidae, Amphiumidae, and Necturidae; strongly divided in most Plethodontidae) and without anterior wings (anterior wings in Amphiumidae and Sirenidae). The neural arch is simple (elaborated with aliform processes in Sirenidae), and the neural spine is weakly developed (strongly developed in some Salamandridae, Amphiumidae, and Sirenidae; obsolete in the Hynobiidae).

Tihen (1958) found that the vertebrae of the Ambystomatidae and the Hynobiidae were very similar, except that in the Hynobiidae the articular facet of the transverse process was not often sharply divided into dorsal and ventral portions, and that the ribs were unicipital. But then he goes on to say "This is not a diagnostic family characteristic; some hynobiids have transverse processes with the dorsal and ventral facets completely separated, indistinguishable from those of ambystomatids".

In the present study I am most impressed by the similarity of ambystomatid and hynobiid vertebrae. I can only make the distinction that ambystomatid vertebrae usually appear to have a slightly stronger neural spine and a slightly less depressed neural arch. The following ambystomatid and hynobiid skeletons were studied: *Hynobius nigrescens* (1), *Ambystoma cingulatum* (1), *A. laterale* (3), *A. mabeei* (1), *A. macrodactylum* (1), *A. maculatum* (6), *A. opacum* (2), *A. rosaceum* (1), *A. talpoideum* (2), *A. texanum* (4), *A. tigrinum* (13), and *Dicamptodon ensatus* (1).

Ambystoma tihenii sp. nov.

Holotype. Trunk vertebra, Saskatchewan Museum of Natural History No. 1431 (Fig. 1a). From early Oligocene, Cypress Hills formation, north branch Calf Creek, in L. S. 4, sec. 8 twp. 8, range 22, W. 3rd mer., el. 3,600 ft. Matrix of conglomeratic sandstone and sands with included clay pellets. Collected by Bruce McCorquodale, A. E. Swanston, and Robert D. Weigel, August, 1963.

Paratype. Trunk vertebra (SMNH 1432, Fig. 1b). Taken by the same collectors at the same locality.

Diagnosis. An *Ambystoma* similar in size and in vertebral proportions to the *Ambystoma opacum* species group of Tihen (1958, p. 19, Table 1), but differs in having (1) the neural arch more depressed, (2) the foramina on the ventral part of the centrum obsolete or absent, (3) the ends of the centrum less widely flared, and (4) the transverse processes usually more robust.

Etymology. The species is named in honor of Dr. J. A. Tihen in recognition of his contributions to the knowledge of the osteology of fossil and recent ambystomatid salamanders.

Description of holotype. In dorsal view: Prezygapophyseal facets ovaloid, about twice as long as wide; neural arch depressed, neural spine low and thin; centrum extending anterior to anterior edge of neural arch; posterior tip of neural arch ending slightly behind posterior edge of poszygapophyses; transverse processes quite robust, slightly backswept, with their articular facets sharply divided into dorsal and ventral portions. In ventral view: Prezygapophyses ovaloid, extending well beyond anterior end of centrum; centrum constricted at its middle, with its ends only moderately flaring; foramina in centrum obsolete; ventral segment of transverse processes more anteriorly directed than dorsal segment;

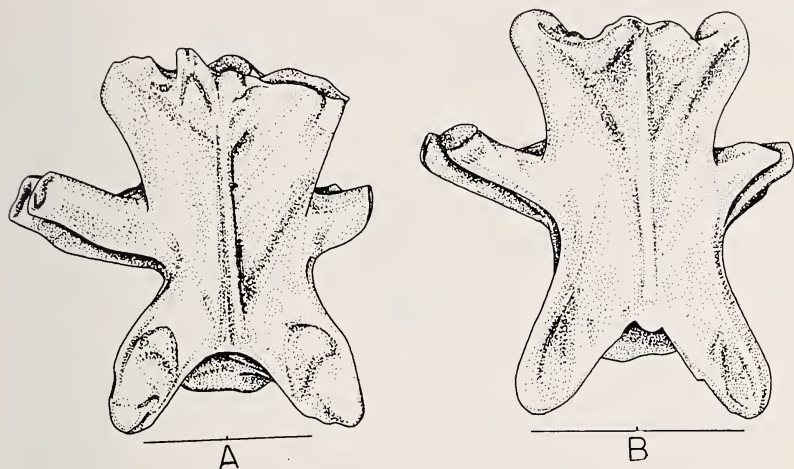


Fig. 1. A, holotype trunk vertebra (SMNH 1431) of *Ambystoma tiheni* sp. nov. in dorsal view; B, paratype trunk vertebra (SMNH 1432) of *Ambystoma tiheni* sp. nov. also in dorsal view. Each line equals 2 mm.

postzygapophyseal faces rounded. Measurements and ratios: length through zygapophyses 4.2 mm, width through prezygapophyses 2.7 mm, width through postzygapophyses 2.8 mm, combined zygapophyseal width divided by length through zygapophyses 1.31.

Description of paratype. Differences between the paratype and the holotype are slight and attributable to individual or to intra-columnar variation. The neural arch ends at the level of the posterior edge of the postzygapophyses. The neural spine is slightly thicker, and the transverse process is slightly less robust. No foramina are discernable on the ventral side of the centrum. Measurements and ratios: length through zygapophyses 3.8 mm, width through prezygapophyses 2.6 mm, width through postzygapophyses 2.4 mm, combined zygapophyseal width divided by length through zygapophyses 1.50.

Remarks. The fossil vertebrae fit best with the *A. opacum* species group (*A. opacum* and *A. talpoideum*) on the basis of size and vertebral proportions. But the fossil differs on the basis of some qualitative characters. Definite assignment of *Ambystoma tiheni* to the *opacum* group should await more fossil material from Oligocene deposits as well as from the long period of time between

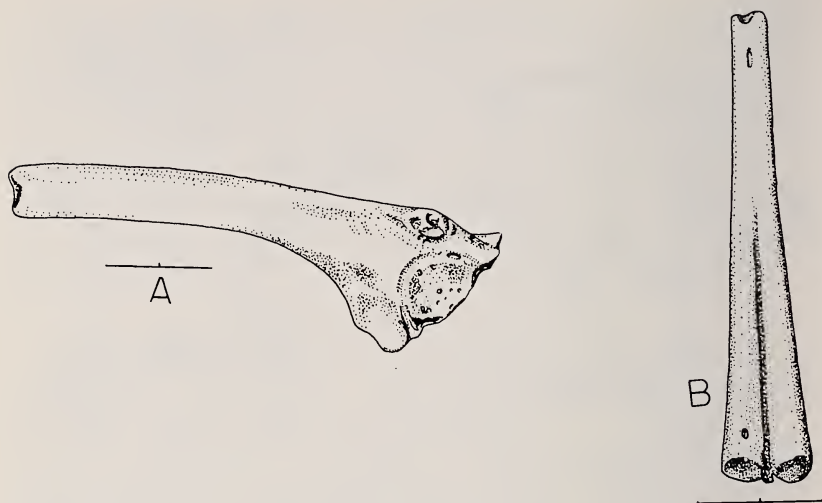


Fig. 2. A, holotype left ilium (SMNH 1435) of *Hyla swanstoni* sp. nov.; B, referred partial tibio-fibula (SMNH 1437). Each line equals 2 mm.

early Oligocene and recent times. Nevertheless, the mere suggestion that species groups of *Ambystoma* were established by early Oligocene times is of considerable interest.

Family RHINOPHRYNIDAE

The sole living species of this family is a burrowing, anteating frog that seemingly comes to the surface only after extremely heavy rains, and that occurs from extreme southern Texas to Central America as far south as Costa Rica. An extinct rhinophrynid genus, *Eorhinophrynus septentrionalis* Hecht is known on the basis of an atlas from the middle Eocene of the Bridger formation of Wyoming (Hecht, 1959). The following species was previously reported from the Cypress Hills by Holman (1963).

Rhinophrynus canadensis Holman

Previous material. Four ilia (one was holotype), two distal femora, and one distal humerus (measurements in Holman, 1963, p. 706-707).

New material. One vertebra, 10 humeri, 4 radio-ulnae, 30 femora, 12 tibio-fibulae, six tarsals, 21 ilia (SMNH 1433).

Remarks. In the present study, 16 recent *Rhinophrynus dorsalis* from a single breeding assemblage in Veracruz, Veracruz, Mexico, taken August, 1965, were compared with *R. canadensis* material.

In the recent skeletons the vertebral centra, other than those of the atlas and sacrum, are hour-glass-shaped, biconcave discs, with their notochordal canals large, and in most specimens, completely open. The only evidence of the presence of the intervertebral bodies of Walker (1938) lies in the anterior concavities of the centra, which are partially filled or encircled by roughened bone. The posterior concavities of the centra are much better excavated and entirely lack a bony filling. In one specimen (2279) the anterior concavities of two vertebral centra are completely plugged with roughened bone. Two other specimens (2275 and 2276) each have a single vertebra in this condition. These are the only vertebrae in the 16 specimens (atlases and sacra not included) that lack a perforate centrum.

A single fossil has a biconcave, completely perforate centrum and represents a frog of about the size of those represented by the other rhinophrynid elements. But the vertebra is so badly worn that many details of structure are obscured, thus it is only tentatively assigned to *R. canadensis*.

The humeri of recent and fossil *Rhinophrynus* are quite characteristic. The previous fossil humerus was only a distal end, but the new material is much more complete. In both living and fossil *Rhinophrynus* the humeri are short and stout and are not only bowed dorsoventrally, but laterally as well. Two distinct ridges occur on the posterior face of the shaft; a long lateral ridge that runs about three-fourths the length of the shaft, and a shorter medial one that runs about one-third the length of the shaft. But the humeri of the fossils are not as short and stout as those of the recent specimens, and the fossils have less robust processes and ridges, a less robust condyle, and they are less laterally bowed than the recent specimens. The radio-ulnae of the fossil species are also less robust than the recent species.

The ilia of *R. canadensis* have previously been described (Holman, 1963). The new species do not differ trenchantly from the original ones. It is interesting to note that the ilia of the fossils do

not seem to be less strong or robust than those of the recent *R. dorsalis*.

Most of the femora of the fossils are much less robust than in recent *R. dorsalis*, with the condyles on the distal end of the femur weak and the two ridges for muscle attachment on the shaft weaker than in recent *R. dorsalis*. But a few of the larger fossils are almost as robust as the recent bones. The tibio-fibulae of recent and fossil *Rhinophrynus* are quite characteristic, being exceptionally short and stout, and with expanded ends. Unfortunately, the fossils are rather fragmentary and worn, and it is difficult to make sharp comparisons with the recent specimens. It does appear that the fossils are less robust than the recent bones.

Measurements of femora and humeri of *Rhinophrynus canadensis* compared with seven *R. dorsalis* from undesignated localities and with the 16 *R. dorsalis* from the breeding population in Veracruz, Veracruz, Mexico (Table 1) show that *R. canadensis*

TABLE 1

Measurements in mm of recent fossil *Rhinophrynus* (means in parentheses)

	Greatest distal width of femur	Greatest distal width of humerus
<i>R. canadensis</i> Oligocene	2.2-4.0 (2.73) n 27	1.8-3.0 (2.46) n 10
<i>R. dorsalis</i> Veracruz	3.4-4.4 (3.91) n 15	2.9-4.2 (3.74) n 16
<i>R. dorsalis</i> Mexico, locality unknown	4.9-6.5 (5.65) n 7	4.6-6.0 (5.36) n 7

may have been a smaller frog than *R. dorsalis*, but probably not as much smaller as previously thought (Holman, 1963).

The fact that several of the bones of the appendicular skeleton of *R. dorsalis*, including the humerus, are shorter and stouter, and have less expanded ends and robust processes; and that the humeri of *R. dorsalis* are more bowed than the fossil species may indicate that the living form is more adapted for burrowing than the fossil species.

Family PELOBATIDAE

This family presently occurs in the United States and Mexico, in Eurasia, the western part of the Indo-Australian Archipelago, the Philippines, and the Seychelles.

Fossil material, not yet studied in detail or described taxonomically, indicates the family Pelobatidae was present by early Cretaceous times. Nevo (1956) reports frogs from the lower Cretaceous of Israel with pelobatid features. Estes (1964) reports "Pelobatidae" from the late Cretaceous Lance formation of eastern Wyoming.

Pelobatids are well known from the Cenozoic of Europe and North America, and one form, *Macropelobates*, is known from the Oligocene of Mongolia (Noble, 1924). Recent studies by Zweifel (1956) and Kluge (1966) have dealt with relatively complete fossils from the middle and late Cenozoic. Kluge points out that the lower Miocene form, *Scaphiopus neuter*, appears to be phylogenetically near the point of divergence of the North American genera *Scaphiopus* and *Spea*, and that the two subgenera probably originated by the Oligocene.

Richard Estes of Boston University is presently reviewing fossil pelobatids, and he has examined and identified the pelobatid remains from the Cypress Hills. He reports to me (*in litt.*) that the Cypress Hills pelobatid is the same species that he is planning to describe from the lower Oligocene of North Dakota. Since this North Dakota form is represented by a complete skull and vertebral column, I will defer designating the Cypress Hills form to species. According to Dr. Estes, the pelobatids from the lower Oligocene of North Dakota and from Cypress Hills represent the subgenus *Scaphiopus* rather than *Spea*, and they are very similar to recent *Scaphiopus holbrooki holbrooki*. This indicates the possibility that there were perhaps at least an Eocene dichotomy of the two subgenera.

Scaphiopus sp.

Material. One frontoparietal, 16 maxillary fragments, 24 vertebrae, 7 humeri, 8 radio-ulnae, 3 sacrococcyges, 71 ilia (37 left and 34 right), 7 tibio-fibulae (SMNH 1434).

Remarks. The frontoparietal bone is relatively complete and well-preserved. It has dermal encrustations present and lacks the

frontoparietal fontanelle as in the subgenus *Scaphiopus*. Kluge (1966) reports that the subgenus *Spea* lacks the dermal encrustation and that it has the frontoparietal fontanelle. The bone is 12.5 mm in length. The 16 maxillary pieces are so fragmentary that it is impossible to accurately discern the shape and extent of their pterygoid processes.

Among the seven humeri is a very large specimen that represents a distal end with a greatest width of 8.3 mm. The three sacrococcyges are quite fragmentary and worn. The most complete of the three has a moderate degree of postsacral webbing, a condition somewhat similar to "category D" of Kluge (1966, Fig. 7). The other two bones are so worn that it is difficult to determine the degree of webbing present. Most of the ilia are fragmentary. In those ilia with the area that bears the dorsal protuberance of Estes and Tihen (1964) in tact, this protuberance was absent in 22, small in 17, and moderately developed in only six. Kluge has provided information about the relative development of the dorsal protuberance in recent species of *Pelobates* and *Scaphiopus*. Because of the fragmentary nature of the ilia it was very difficult to find a measurement that would be standard in all of the bones. The greatest height of the acetabular cup appears to best reflect the size of the bones. This distance is 1.6-4.7 mm (mean, 3.07) in the 29 measureable specimens.

Family HYLIDAE

This family has a wide distribution at present, ranging through the New World, Australia and New Guinea, part of Europe, Asia north of the Himalayas, and Africa north of the Sahara.

The early part of the fossil record of the group is not clear. Estes (1964) reports "Family *incertae sedis*, near Hylidae?" from the late Cretaceous Lance formation of eastern Wyoming. In the Tertiary, *Amphignathodon* of the early Oligocene of Europe was referred to the Hylidae by Piviteau (1927), but this fossil may consist of a mixture of anuran and lizard elements (Chantell, 1964) and needs re-study.

Modern hylid genera are first known from the early Miocene of Europe (Schaeffer, 1949) and North America (Auffenberg, 1956 and Holman, 1967) with only one genus (*Proacris*) considered to be extinct (Holman, 1961). Hylids of late Miocene through Pleis-

tocene times all represent modern genera and are similar or identical to recent species (Chantell, 1964, Gehlbach, 1965, Holman, 1966).

The following skeletons were studied in the identification of the hylid material from Cypress Hills: *Acris crepitans* (15), *A. gryllus* (6), *Anotheca coronata* (2), *Diaglena reticulata* (2), *Gastrotheca marsupiata* (1), *Hyla arenicolor* (7), *H. californiae* (2), *H. cinerea* (4), *H. crucifer* (3), *H. ebraccata* (1), *H. elaeochroa* (5), *H. eximia* (2), *H. femoralis* (2), *H. gratiosa* (3), *H. miotympanum* (5), *H. phaeocrypta* (2), *H. regilla* (6), *H. septentrionalis* (1), *H. squirella* (10), *H. versicolor* (10), *H. wrightorum* (1), *Limnaeodius ocularis* (3), *Pseudacris nigrita* (8), *P. ornata* (1), *P. streckeri* (14), *P. triseriata* (10), *Phrynohyas spilomma* (2), *Phyllomedusa dacnicolor* (3), *Pternohyla fodiens* (3), *Smilisca baudini* (9), and *S. phaeota* (1). Terminology for the *Hyla* section follows Chantell (1964).

Hyla swanstoni sp. nov.

Holotype. Left ilium, Saskatchewan Museum of Natural History No. 1435 (Fig. 2a). From early Oligocene, Cypress Hills formation, north branch of Calf Creek, in L. S. 4, sec. 8, twp. 8, range 22 W. 3rd mer., el. 3,600 ft. Matrix of conglomeratic sandstone and sands with included clay pellets. Collected by Bruce McCorquodale and A. E. Swanston.

Paratype. Left ilium (SMNH 1436) from the same locality and taken by the same collectors.

Referred material. Three partial tibio-fibulae (SMNH 1437, Fig. 2b).

Diagnosis. A *Hyla* ilium similar to *Hyla miofloridana* Holman of the lower Miocene of Florida in its weakly developed dorsal protuberance and in having a groove on the lateral border of the ilium just anterior to the acetabulum, but differing from this species in being smaller, and in having the groove shallower and with an indistinct ventral border.

Etymology. The fossil is named in honor of A. E. Swanston of the Saskatchewan Museum of Natural History in recognition of his work in vertebrate paleontology.

Description of holotype. The anterior border of the dorsal protuberance ends slightly anterior to the level of the anterior border

of the acetabulum, and the protuberance is ovaloid and with its long axis horizontal. Part of the dorsal protuberance has been eroded, but it is weakly developed and projects more laterad than dorsad. The distance between the ventral border of the dorsal protuberance and the border of the acetabulum is only about one-fourth the length of the protuberance. The dorsal acetabular expansion has its tip broken. The acetabular area is rather worn, but the acetabulum is rather weakly excavated. The acetabular border is quite worn. The ventral acetabular expansion is moderately wide and its anterior border makes an angle of much greater than 90 degrees with the shaft. The tip of the ventral acetabular expansion is broken. There is no dorsal ridge or crest on the compressed ilial shaft. A shallow groove that lacks a distinct ventral border lies on the lateral face of the ilial shaft just anterior to the acetabulum. Measurements: greatest height of ilial shaft 1.3 mm, height of acetabular fossa 1.7 mm, length of dorsal protuberance 1.0 mm.

Paratype. The paratype is more worn than the holotype, but it appears to represent another individual of the same species. The dorsal protuberance is completely broken off and is represented only by a scar. Moreover, the dorsal prominence is eroded. But based on the scar left by the dorsal protuberance, the anterior border of this structure seems to have been slightly farther forward on the bone than in the holotype. Moreover, the lateral groove is somewhat more distinct. But both these differences seem attributable to individual variation. The border of the acetabulum is highly worn and the tips of the dorsal and ventral acetabular expansions are broken in the paratype. Measurements: greatest height of shaft 1.4 mm, height of acetabular fossa 1.6 mm.

Referred elements. The tibio-fibulae represent frogs of about the same size as those represented by the ilia and are of the same elongate proportions as in tibio-fibulae in recent hylid frogs. Thus, these bones are tentatively referred to *Hyla swanstoni*.

Remarks. Holman (1967) discussed characters of the ilia of various hylid genera and described *Hyla miofloridana* from the early Miocene of Florida, a form that shows similarities to recent *Hyla cinerea*, *H. gratiosa*, and *H. versicolor*. The chief difference between *H. miofloridana* and the recent species is that the dorsal protuberance of the fossil is less produced and distinct from the

shaft than in the recent forms and that a groove with a strong ventral border on the lateral face of the ilial shaft just anterior to the acetabular fossa is present in the Miocene fossil. A second early Miocene *Hyla* from the same deposit was described by Auffenberg (1956) and re-studied by Holman (1967). This smaller form, *Hyla goini*, has a strong dorsal protuberance, lacks the lateral groove, and is rather similar to *Hyla squirella*, a small tree frog that is common in Florida today. *Hyla swanstoni* is more similar to *H. miosfloridana* than to *H. goini* in having a weakly developed dorsal protuberance and a lateral groove present. The fact that the earliest known North American frogs of the family Hylidae are referable to the genus *Hyla* is of considerable interest.

DISCUSSION AND SUMMARY

The modern nature of the amphibian fauna of the early Oligocene of the Cypress Hills formation is striking. All of the genera are living at present, and modern subgenera, and in some cases even modern species groups, may have been differentiated by early Oligocene times.

Another interesting aspect of the Cypress Hills fauna is the absence of the ubiquitous genera *Rana* and *Bufo*. These genera, especially the former, are almost without exception the most abundant anuran remains in late Cenozoic fossil faunas, yet neither genus is represented among hundreds of individual bones and fragments from the Cypress Hills.

Ambystoma tihen represents the subgenus *Ambystoma* and has vertebral proportions similar to the *opacum* species group of Tihen (1958). But whether these vertebral proportions indicate an actual relationship to the *opacum* group may be conjectural. Today, the *opacum* group is restricted to the United States east of the great plains. Another species group, the *maculatum* group, is quite similar to the *opacum* group in most respects, and although it differs in vertebral proportions, it may be related to the fossil. The *maculatum* group has a disjunct distribution today. One part of the group occurs along the Pacific coast from southern Alaska to northern California and east into Montana; another part occurs in the east from southern Labrador to southeastern Manitoba and south throughout most of the United States east of the great

plains. It would seem that the fossil could be ancestral to either the *opacum* group or the *maculatum* group or perhaps to both.

The new *Rhinophrynus canadensis* material indicates that the fossil form is a more distinct species than was formerly thought, but not as much smaller than the recent form as was previously believed. The facts that the humeri, radio-ulnae, femora, and tibulae are more elongate, the humeri less bowed, and all of these bones less robust, may indicate that the fossil was less adapted for burrowing than the recent species. But I see no evidence to indicate that *R. canadensis* was not directly ancestral to *R. dorsalis*. Today, *R. dorsalis* occurs from Zapata County, in extreme southern Texas, south through Mexico to Costa Rica. It apparently occurs on both coasts in Mexico. I suspect that this range reflects a withdrawal of the species from the north during the deterioration of the climate during the middle and late Tertiary.

The fact that the *Scaphiopus* material can be relegated to subgenus with confidence and is similar to the living species, *Scaphiopus holbrooki* is of much interest. Perhaps the subgenera *Scaphiopus* and *Spea* may have differentiated in the Eocene or earlier rather than the Oligocene dichotomy that was previously suggested by Kluge (1966). Today, *S. holbrooki* ranges mainly east of the 100th Meridian in the United States with only one extralimital population (*S. h. hurteri*) occurring in the panhandle areas of Texas and Oklahoma. But the subgenus *Spea* (*S. bombifrons*) is the only pelobatid that occurs in Saskatchewan today. This situation parallels the one in the fossil *Ambystoma* where the recent species group most similar to the fossils occurs in eastern United States.

The presence of *Hyla* from the early Oligocene of Saskatchewan indicates the possibility of an Eocene or earlier origin of modern hylid genera. *Hyla swanstoni* is similar to several species of *Hyla* living in eastern United States in the middle Cenozoic and in recent times. This Oligocene fossil may be close to the ancestry of *Hyla m'offloridana* of the early Miocene of Florida.

Paleoecological inferences in many cases must be based on ecological patterns of living species that are closely related or identical to fossil ones. Fortunately, the early Oligocene fossils are taxonomically similar to forms living today, and such inferences can be made. The most abundant anurans are *Rhinophrynus cana-*

densis and *Scaphiopus* sp. Both of these animals suggest a climate where rainfall was sporadic and seasonal. Recent *Rhinophrynus dorsalis* is characterized by being especially dependent upon torrential, even violent rainstorms to initiate breeding. Many field workers, including myself, have been impressed with the fact that the only time one can expect to collect *R. dorsalis* is immediately after particularly heavy seasonal rains. Several workers have also noticed that *Scaphiopus holbrooki*, a form closely related to the fossil, does not have a particular breeding cycle, but rather breeds after heavy rains. Moreover, they breed in temporary water and their tadpoles metamorphose very quickly. Bragg (1945) has cited this as characteristic of xeric breeding patterns in amphibians. Thus, I think it is possible to postulate that during the Oligocene the Cypress Hills area was characterized by a fairly xeric climate with seasonal rainfall. The presence of crocodilians, boid snakes, *Rhinophrynus*, and *Scaphiopus* in the same fauna suggests a climate not unlike that of the coastal lowlands of Mexico today.

LITERATURE CITED

- AUFFENBERG, W. 1956. Remarks on some Miocene anurans from Florida, with a description of a new species of *Hyla*. *Breviora*, no. 52, pp. 1-11.
- BRAGG, A. N. 1945. The spadefoot toads of Oklahoma with a summary of our knowledge of the group, II. *American Nat.*, vol. 79, pp. 52-72.
- COPE, E. D. 1891. On vertebrata from the Tertiary and Cretaceous rocks of the Northwest Territory, I. The species from the Oligocene or Lower Miocene beds of the Cypress Hills. *Geol. Surv. Canada, Contrib. Canadian Paleontol.*, vol. 3, pt. 1, pp. 1-25.
- CHANTELL, CHARLES J. 1934. Some Mio-Pliocene hylids from the Valentine formation of Nebraska. *American Midl. Nat.*, vol. 72, no. 1, pp. 211-225.
- ESTES, RICHARD. 1964. Fossil vertebrates from the late Cretaceous Lance formation eastern Wyoming. *Univ. California Pubs. Geol. Sci.*, vol. 49, pp. 1-180, 5 pls.
- ESTES, RICHARD, AND J. A. THIEN. 1964. Lower vertebrates from the Valentine formation of Nebraska. *American Midl. Nat.* vol. 72, no. 2, pp. 453-472.
- GEHLBACH, FREDERICK R. 1965. Amphibians and reptiles from the Pliocene and Pleistocene of North America: A chronological summary and selected Bibliography. *Texas Jour. Sci.*, vol. 27, no. 1, pp. 56-70.

- HOLMAN, J. A. 1961. A new hylid genus from the lower Miocene of Florida. *Copeia*, 1961, no. 3, pp. 354-355.
- . 1963. A new rhinophrynid frog from the early Oligocene of Canada. *Copeia*, 1963, no. 4, pp. 706-708.
- . 1965. A late Pleistocene herpetofauna from Missouri. *Trans. Illinois Acad. Sci.* vol. 58, no. 3, pp. 190-194.
- . 1966. A small Miocene herpetofauna from Texas. *Quart. Jour. Florida Acad. Sci.* vol. 29, no. 4, pp. 267-275.
- . 1967. Additional Miocene anurans from Florida. *Quart. Jour. Florida Acad. Sci.* vol. 30, no. 2, pp. 121-140.
- HECHT, M. K. 1959. Amphibians and reptiles, in Paul O. McGrew, The geology and paleontology of the Elk Mountain and Tabernacle Butte area, Wyoming. *Bull. American Mus. Nat. Hist.*, vol. 117, art. 3, pp. 117-176, 27 figs., 7 pls., 15 tables.
- KLUGE, ARNOLD G. 1966. A new pelobatine frog from the lower Miocene of South Dakota with a discussion of the evolution of the *Scaphiopus-Spea* complex. *Los Angeles County Mus. Contr. Sci.* no. 113, pp. 1-26.
- LAMBE, L. M. 1908. The vertebrata of the Oligocene of the Cypress Hills, Saskatchewan. *Geol. Surv. Canada Contrib. Canadian Paleontol.*, vol. 3, pt. 4, pp. 1-65.
- McCONNELL, R. G. 1885. Report on the Cypress Hills, Wood Mountain and Adjacent Country. *Geol. Surv. Canada, Ann. Rept.*, vol. 1, pt. c, 85 pp., 3 pls., 1 map.
- NEVO, ABIATHA R. 1956. Fossil frogs from a lower Cretaceous bed in southern Israel (Central Negev). *Nature*, vol. 178, pp. 1191-1192.
- NOBLE, G. K. 1924. A new spadefoot toad from the Oligocene of Mongolia with a summary of the evolution of the Pelobatidae. *American Mus. Nov.*, no. 132, pp. 1-15.
- PEABODY, FRANK E. 1954. Trackways of an ambystomatid salamander from the Paleocene of Montana. *Jour. Paleontol.*, vol. 28, no. 1, pp. 79-83.
- . 1959. Trackways of living and fossil salamanders. *Univ. California Pubs. Zool.*, vol. 63, pp. 1-72.
- PIVETEAU, J. 1927. Etudes sur quelques amphibiens et reptiles fossiles. *Ann. Paleontol.*, no. 16, pp. 57-97.
- RUSSELL, LORIS S. 1934. Revision of the lower Oligocene vertebrate fauna of the Cypress Hills, Saskatchewan. *Roy. Canadian Inst. Trans.*, vol. 20, pt. 1, pp. 49-67.
- . 1936. New and interesting mammalian fossils from western Canada. *Roy. Soc. Canada Trans.*, 3rd ser., vol. 30, sec. 4, pp. 75-80.

- . 1938. The skull of *Hemipsalodon grandis*, a giant Oligocene creodont. Roy. Soc. Canada Trans., 3rd ser., vol. 32, sec. 4, pp. 61-66.
- . 1940. Titanotheres from the lower Oligocene Cypress Hills formation of Saskatchewan. Roy. Soc. Canada Trans., 3rd ser., vol. 34, sec. 4, pp. 89-100.
- . 1948. Geology of the southern part of the Cypress Hills, southwestern Saskatchewan. Sask. Dept. Min. Rep. no. 8, pp. 1-60.
- SCHAEFFER, B. 1949. Anurans from the early Tertiary of Patagonia. Bull. American Mus. Nat. Hist. vol. 93, no. 2, pp. 41-68.
- TIHEN, J. A. 1958. Comments on the osteology and phylogeny of ambystomatid salamanders. Bull. Florida State Mus. Biol. Sci. Ser., vol. 3, no. 1, pp. 1-50.
- TIHEN, J. A., AND C. J. CHANTELL. 1963. Urodele remains from the Valentine formation of Nebraska. Copeia, 1953, no. 3, pp. 505-510.
- WALKER, CHARLES F. 1938. The structure and systematic relationships of the genus *Rhinophrynus*. Occ. Papers Mus. Zool. Univ. Michigan, no. 372, pp. 1-11.
- WEIGEL, ROBERT D. 1963. Oligocene birds from Saskatchewan. Quart. Jour. Florida Acad. Sci., vol. 26, no. 3, pp. 257-262.
- ZWEIFEL, RICHARD G. 1956. Two pelobatid frogs from the Tertiary of North America and their relationships to fossil and recent forms. American Mus. Nov. no. 1762, pp. 1-45.

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